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Morphological shifts in populations of generalist and specialist amphibians in response to fragmentation of the Brazilian Atlantic forest

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Abstract

Changes in morphological traits, such as body size, body condition, and leg length, are important indicators of changes to life history or habitat quality, which can affect the performance of individuals and therefore the persistence of populations under environmental change. Only very few studies assessed the effect of fragmentation on morphological traits. The few available studies on anurans found that in landscapes with less forest cover body size decreased. Therefore, we predict that body size should also be smaller in fragments compared to continuous forest. Body condition is a further trait closely related to individual performance and thus should decline with more adverse conditions, as is expected in fragments. We tested these hypotheses using snout-vent length, body mass, body condition, and tibia length as response variables. We collected data of a habitat generalist (*Rhinella ornata*) and a habitat specialist (*Ischnocnema guentheri*), both leaf-litter amphibian species, from three sites in a fragmented landscape (two isolated and one connected site) and one site in a contiguous part of the Atlantic Forest of Southeast Brazil. In the generalist species, snout-vent-length (SVL) and body mass were significantly lower in fragments compared to the contiguous forest control, whereas tibia length and body condition

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did not differ among sites. In contrast, SVL, body mass, and tibia length of the specialist species did not differ among sites, but body condition was marginally different among sites, being relatively low in one but not the other isolated fragment. The results indicate that different processes affect the morphology of the two species following habitat fragmentation.

Keywords
Fragmentation, habitat loss, amphibians, body size, body condition, Brazilian Atlantic forest

Introduction

Habitat loss and fragmentation are a major cause of biodiversity loss (Sarre et al. 1996, Pimm and Raven 2000, Sala et al. 2000, Funk and Mills 2003, Henle et al. 2004). Most studies examining their effects focused on community composition, patch occupancy patterns, population viability, and the genetic variability of selected species (e.g. Tocher et al. 1997, Wiegand et al. 2001, Bell and Donnelly 2006, Dixo et al. 2009, Tucker et al. 2014). In contrast to the large volume of literature for oceanic islands (e.g. Kramer 1951, Losos 2009), very few studies addressed changes in morphological parameters following habitat fragmentation. However, habitat loss leads to major changes in abiotic and biotic conditions and morphology is known to respond to abiotic and biotic conditions (Wade 2004). Exemplarily, Smith et al. (1997) found that differences in vegetation structure between African rainforest and the rainforest-savanna ecotone led to different selection regimes causing morphological changes in rainforest birds.

Changes in morphological factors are important indicators of changes in life history or habitat quality (Palkovacs 2003, Buckley et al. 2005, Lowe et al. 2006, Lomolino and Perault 2007). Snout-vent-length, body condition, and body proportions are important phenotypic factors that affect the performance of individuals in terms of their reproductive output and survival in numerous organisms (Stearns 1976, Roff 1992). In amphibians, smaller snout-vent length and lower body condition often translate into reduced survival probability (Altwegg and Reyer 2003) and cause maternal effects, such as poor clutch quality (Reading 2007), smaller clutch size (Funk and Mills 2003), and smaller egg size (Kaplan 1992, Laugen et al. 2002). These factors in turn lead to a lower number of hatchlings and metamorphosing individuals (Berven and Gill 1983, Semlitsch et al. 1988) and affect the size at metamorphosis (Pakkasmaa et al. 2003, Räsänen et al. 2005), maturity, and fecundity (Smith 1987, Semlitsch et al. 1988). As a consequence of their important influence on demographic traits, body size and body condition may ultimately determine the ability of species to persist under changed environmental conditions.

Various environmental factors are known to influence morphology and body condition. In amphibians, resource availability, predation risk, and temperature during larval development have been frequently identified as major determinants of body size and body condition. An increase in resource availability can lead to better body condition and a larger body size (e.g., Du 2006, Jessop et al. 2006, Wu et al. 2006). Due to the costs of anti-predator behaviour, higher predation pressure can lead to early hatch-

ing, lower growth and developmental rates, and thus to a smaller size at emergence or metamorphosis (e.g., Ball and Baker 1996, Laurila et al. 2002). In amphibians this further negatively affects limb dimensions and locomotor performance (Goater et al. 1993, Buckley et al. 2005). Warmer temperatures accelerate developmental processes and usually lead to an earlier metamorphosis, smaller size at metamorphosis, smaller size at maturity, and therefore overall a smaller adult size (Smith 1987, Semlitsch et al. 1988, Beachy 1995, Ståhlberg et al. 2001).

Habitat loss and fragmentation create changes in the abiotic and biotic environment, therefore leading to changes in the quality of the remaining habitat (Saunders et al. 1991) that can result in changing selective pressures on morphology (Thomas et al. 1998, Ewers and Didham 2006). Thus, changes in morphology may serve as an early and easy to measure indicator for negative effects of fragmentation on species (Sumner et al. 1999). Finding suitable early indicators of environmental stress (Helle et al. 2011) is important in order to apply effective conservation measures prior to severe declines of populations and of the species at the landscape level (Leary and Allendorf 1989). However, the contribution of habitat loss and fragmentation to phenotypic changes is poorly known, in particular in amphibians. Neckel-Oliveira and Gascon (2006) showed shifts in the body size of a habitat generalist (*Phyllomedusa tarsius*) in fragments, regrowth forest, and pasture compared to continuous forest, with larger individuals in the latter, and explained these shifts with changes in habitat quality. Leg-length in relation to snout-vent length was also affected by the degree of retained forest in one Neotropical frog species (Delgado-Acevedo and Restrepo 2008). Likewise, the prickly forest skink (*Gnypetoscincus queenslandiae*) of tropical Australia was smaller and had lower mass (corrected for differences in snout-vent-length) in fragments compared to continuous forests (Sumner et al. 1999).

Body condition declined and the level of stress hormones increased with the number of forest fragments in a study of the common toad (*Bufo bufo*) (Janin et al. 2011). Likewise, yellow-bellied toads (*Bombina variegata*) from forest ponds showed better body condition than those from ponds in the agricultural matrix (Scheele et al. 2014). In contrast, Püttker et al. (2008) found a negative relationship between body condition and patch size in two tropical forest small mammal species that are habitat specialists and no significant relationship in four species that are habitat generalists. The mechanism(s) driving these patterns remain unclear but likely involve multiple factors.

Since previous studies found that in more disturbed habitats and landscapes with less forest cover body size decreased in anurans (Pyastolova and Vershinin 1999, Neckel-Oliveira and Gascon 2006, Delgado-Acevedo and Restrepo 2008), we predict that body size should also be smaller in fragments compared to continuous forest. Due to the strong link among morphological characteristics, we further predict that leg length and body condition should be reduced in forest fragments compared to continuous forest. Here, we test these hypotheses. Moreover, habitat specialists are particularly sensitive to changes of microhabitat quality in fragmented habitats and are consequently more prone to extinction in the fragmented landscape than generalists (Margules 1996, Henle et al. 2004), we therefore assume a stronger response regarding the morphological shifts of habitat specialist species compared to generalist species.

Material and methods

Study area

The study was carried out in the Mata Atlântica, Brazil, in continuous forest of the Morro Grande Reserve and a fragmented landscape surrounding Caucaia do Alto (both approx. 23°40′S, 47°01′W), located 40 km southwest of São Paulo in the municipalities of Cotia and Ibiúna, Brazil. The forest reserve and the adjacent study area are located on the Atlantic Plateau of São Paulo at an altitudinal range of 860-1075 m above sea level (Metzger et al. 2006). The original forest of the study region is classified as lower montane rainforest and forms a transition between the coastal Atlantic rain forest and the Atlantic semi-deciduous forest (Oliveira and Fontes 2000). All study sites, including the control site, were characterised by secondary forest and have remained undisturbed for at least 50 years. The fragmented landscape presented approx. 31% of remaining, highly fragmented forest that was surrounded by urban areas and rural installations (15%) and open areas (i.e., agriculture, pasture, fallow lands, areas in early successional stages; 39.3%) (see Dixo et al. 2009).

We selected four sites: two isolated small forest fragments (Carmo Messias and Dito, referred to in the following as "iso1" and "iso2", respectively), one small forest fragment (Alcides, referred to in the following as "connect") connected by a forest corridor to a larger forest area, and a control site ("control") within the continuous forest. Forest fragments covered an area of 5 ha each and contained no permanent/larger water bodies within the forest area or within a radius of 200 m outside the forest fragment. The continuous forest was about 9,400 ha in size. There was no permanent/larger water body present at the control site within a radius of 200 m.

Selected species

We chose two leaf-litter dwelling forest species for comparison. We selected *Rhinella ornata*, a bufonid species, as a habitat generalist due to its high tolerance to matrix habitats. This species is distributed throughout the Atlantic Forest in the states of São Paulo and Rio de Janeiro (Haddad et al. 2008) and can be found in undisturbed continuous forest areas as well as in disturbed forest fragments (Heyer et al. 1990). It breeds in temporary and permanent ponds within forests and open areas (Izecksohn and de Carvalho-e-Silva 2001, Haddad and Prado 2005). Reproduction starts at the end of the dry season in late July and at the beginning of August (Dixo 2005).

We selected *Ischnocnema guentheri* for comparison. This species is distributed over large parts of the Mata Atlântica (Haddad et al. 2008) and occurs only within forest habitats although it can sometimes be encountered in vegetation close to the forest edge (Heyer et al. 1990). Thus, it has a more specialised habitat requirement. Females deposit egg clutches terrestrially, hidden below tree trunks and stones (Kwet and

Di-Bernardo 1999, Izecksohn and de Carvalho-e-Silva 2001). Frogs develop directly within the egg capsule (Heyer et al. 1990, Izecksohn and de Carvalho-e-Silva 2001).

Sampling

We established three parallel transects of 100 m each on each site. We sampled frogs by hand during the rainy seasons October 2003 until March 2004 and November 2004 until March 2005. We surveyed each site for five consecutive nights (21:00 – 01:00 local time) before sampling the next site. Once all sites had been sampled, the next round of sampling started again at the first site. The total search effort was 25 nights per site (2003/2004 15 nights per site, 2004/2005 10 nights per site).

We measured snout-vent-length (SVL) and tibia length (TL) of all captured individuals using a calliper with an accuracy of ±0.1 mm. We measured tibia length for the left body side. We weighed individuals using digital scales with an accuracy of ±0.1 g. We used photographical individual identification to eliminate data points of recaptured individuals. As juveniles were seldom captured, we only included the data of subadult and adult individuals in the analysis (*R. ornata* with a SVL ≥ 27 mm; *I. guentheri* with a SVL ≥ 10 mm). As knowledge on natural history of both species is scarce, we could not further separate subadult from adult individuals. Unless calling, sexes cannot be separated by external morphology in both species.

Data analysis

Opinions about which body condition index (BCI) to use are controversial in the literature (Jakob et al. 1996, Schulte-Hostedde et al. 2005, Peig and Green 2009). The most common approaches are to use the residuals from a regression of mass on the third power of length or of *ln* mass on *ln* size. Peig and Green (2009) developed a scaled mass index (SMI) which standardizes body mass at a fixed value of body size based on the scaling relationship between mass and body size using major axis regressions. This new index better reflects changing relationships between mass and body size considering different growth curves at different ages than alternative indices (Peig and Green 2009, 2010). We used the SMI and additionally the more frequently used residuals of the regression of *ln* mass on *ln* size for consistency assessment.

We assessed differences in SVL, body mass, and BCI among sites by using an analysis of variance (ANOVA), after testing the assumption of normality of all variables used (Kolmogorov-Smirnov-Test: $D = 0.5 – 0.7$, all $\alpha > 0.05$). For tibia length, we used an analysis of covariance (ANCOVA) to remove a potential influence of SVL in the comparison of sites. For significant results, we used the post-hoc Tukey's Honestly Significant Difference test (Tukey's HSD) for multiple comparisons to assess differences among individual sites.

Results

We captured a total of 499 individuals of the selected species, comprising 116 *R. ornata* and 383 *I. guentheri*. After removing juvenile individuals from the data, 54 and 376 individuals respectively were kept for the analyses. An overview of captures and measurements per species and site is given in Table 1.

In *R. ornata* snout-vent-length (SVL) and mass differed significantly among sites (ANOVA: $F = 5.03$, $\alpha < 0.01$; and $F = 5.7$, $\alpha < 0.$, respectively). Both were highest for the control site, with the difference to "iso1" being statistically significant in a Tukey's HSD ($\alpha < 0.01$) and that to "iso2" being marginally significant ($\alpha = 0.09$) for SVL and significant ($\alpha = 0.05$) for mass. Both were intermediate in the connected small site. Tibia length (TL) did not differ among sites when accounting for differences in SVL (ANCOVA: $F = 0.41$, $\alpha = 0.7$). BCI calculated as SMI did not differ among sites (ANOVA: $F = 0.726$, $\alpha = 0.5$). The same was the case when using residuals of the regression of *ln* mass on *ln* SVL as BCI (ANOVA: $F = 0.64$, $\alpha = 0.9$).

Snout–vent length and body mass of *I. guentheri* did not differ significantly among sites (ANOVA: $F = 1.35$, $\alpha = 0.26$ and $F = 0.84$, $\alpha = 0.47$, respectively). Likewise, TL did not differ significantly among sites when the effect of SVL was accounted for (ANCOVA: $F = 0.84$, $\alpha = 0.5$). BCI based on SMI was highest in the control site and one isolated site and lowest in the other isolated site (Table 1), but the difference among sites was only marginally significant (ANOVA: $F = 2.00$, $\alpha = 0.11$). When using the residuals of the regression of *ln* mass on *ln* SVL as BCI, qualitatively results were very similar though BCI was highest in the control site (data not shown). The difference among sites was marginally significant ($F = 2.67$, $\alpha = 0.09$), but all comparisons between pairs of sites were not significant (Tukey's HSD; all $\alpha > 0.05$).

Table 1. Mean ± one standard deviation (SD) of morphological traits of the studied species in the four study sites. Abbreviations: control = control site, connect = connected site, iso1 and iso2 = isolated site one and two; BCI: body condition; N: sample size; SVL: snout-vent-length; TL: tibia length. [BCI calculated as SMI]

	N	SVL (mm)	TL (mm)	BCI	Body mass (g)
I. guentheri					
control	18	20.0±2.4	13.9±1.5	0.78±0.10	0.74±0.24
connect	60	21.4±4.4	15.0±3.1	0.75±0.20	0.94±0.49
iso1	136	20.2±5.1	14.0±3.9	0.70±0.22	0.84±0.62
iso2	162	19.6±7.0	13.4±5.5	0.78±0.33	0.94±0.86
R. ornata					
control	9	57.8±22.2	26.5±9.2	6.46±0.54	19.9±19.1
connect	6	51.2±12.5	23.9±6.3	6.65±0.72	11.3±5.9
iso1	26	39.4±8.5	18.3±4.0	7.04±1.30	5.3±4.0
iso2	13	44.4±12.2	20.1±6.2	6.61±1.42	8.2±8.0

Discussion

Our results partly support the predicted effects of fragmentation on phenotypic characteristics (smaller snout-vent-length, shorter legs, and lower body mass, and body condition in fragments compared to continuous habitat). Individuals of the generalist species *R. ornata* were smaller in fragmented habitats compared to the control site, while body condition did not differ among sites. For the specialist species *I. guentheri* body condition differed marginally significantly among sites and was highest in the control site and in one isolated fragment but lowest in the other isolated fragment. The other morphological traits did not differ among sites. Thus, the habitat generalist and the habitat specialist showed different morphological responses to habitat fragmentation.

The reduced body size in *R. ornata* and the lower body mass of *I. guentheri* in the most severely affected (small isolated) site(s) are in line with previous studies in lizards and amphibians that found a reduced body size in landscapes with low forest cover, in fragments, and in disturbed compared to undisturbed habitats (Pyastolova and Vershinin 1999, Sumner et al. 1999, Neckel-Oliveira and Gascon 2006, Delgado-Acevedo and Restrepo 2008). Neckel-Oliveira and Gascon (2006) assumed, but did not test, that the morphological difference was environmentally induced during development due to changes in the habitat quality of the larval habitat. A smaller size at metamorphosis frequently translates into a smaller adult body size in anurans (Smith 1987, Semlitsch et al. 1988) although data from tropical species are not yet available. This explanation may also apply to the observed morphological shifts in *R. ornata*, as it also undergoes development in aquatic habitats.

In fragments that do not retain suitable aquatic habitats eggs have to be deposited in water bodies in the matrix. Eggs and aquatic larvae have to deal with changes in biotic and abiotic parameters of reproduction ponds within the matrix. Ponds inside and outside of forests usually will differ in physical conditions (Becker et al. 2007). Ponds within the matrix will receive more insolation and should therefore generally be warmer than forest ponds. Warmer temperatures accelerate developmental processes and usually lead to an earlier metamorphosis, smaller size at metamorphosis, smaller size at maturity, and therefore overall a smaller adult size (Smith 1987, Semlitsch et al. 1988, Beachy 1995, Ståhlberg et al. 2001, Wells 2007).

For frogs with a direct development much less is known about the factors that determine development and the morphology of hatchling and subsequently adult anurans than for pond breeding anurans. Delgado-Acevedo and Restrepo (2008) found smaller individuals of two directly developing *Eleutherodactylus* species – a genus closely related to *Ischnocnema* – in disturbed and fragmented compared to undisturbed and unfragmented habitats. They further found an influence between the level of remaining forest cover in the landscape and the allometric change of leg length in one of the species. We did not find a change in snout-vent-length, leg length, or body mass in *I. guentheri*. Delgado-Acevedo and Restrepo (2008) did not provide an explanation for their observations but laboratory studies in *Eleutherodactylus coqui* showed that froglets from eggs that hatched early had relatively smaller legs than froglets in the control

group (Buckley et al. 2005). More studies on directly developing frogs in fragmented landscapes are required before a clear pattern on morphological changes can emerge and mechanistic explanations can be derived.

The results for body condition suggest that the quality of the terrestrial habitat was not negatively affected for the habitat generalist *R. ornata* despite body mass being significantly lower in isolated fragments. For the habitat specialist *I. guentheri* habitat quality seems to have been negatively affected in one but not the other isolated fragment. This suggests that the study sites differed in food resource quality or physiological stress that translate into energetic costs for the latter species in some fragments but not in others. While fragmentation of tropical forests has a large effect on species composition and abundance in invertebrates (Didham et al. 1998), the majority of anurans are rather opportunistic in their food choice (Toft 1985). However, the study of Didham et al. (1998) suggested that in tropical forests common invertebrate species seem to be more sensitive to fragmentation than rarer species; and edges alter the trophic structure of communities (Laurence et al. 2011). Whether these changes translate into different overall abundances of invertebrates that are suitable as food for medium sized frog species, whether abundance changes differs among fragments and may depend on the matrix, and whether these changes differ for habitat generalists and specialists remain to be studied.

Edge effects on abiotic conditions, such as an increase in temperature and a decrease of humidity, affect a larger fraction of a small than a large patch or continuous forests (Saunders et al. 1991). Habitat generalists that are matrix tolerant may be better adapted to deal physiologically with such changes than forest habitat specialists that are intolerant to the matrix. This may explain why in our study body condition decreased in one isolated fragment in the habitat specialist *I. guentheri* whereas it was not affected in the matrix tolerant *R. ornata*. Similarly, Scheele et al. (2014) explained the higher body condition in the yellow-bellied toad (*Bombina variegata*) in forest ponds compared to ponds in pastures by a combination of higher resource availability, more humid micro-climatic conditions and greater water availability.

In conclusion, the effects of fragmentation on size and body condition differed between the habitat generalist and the habitat specialist. This suggests that the two species are affected by different processes driving morphological shifts in the wake of habitat fragmentation, and that for specialists these processes may differ among fragments. The observation that in the same study region as ours habitat specialists among small mammals showed an increase in body condition with fragmentation (Püttker et al. 2008) further corroborates that fragmentation may affect ecological processes that result in unexpected morphological shifts in species-specific ways. Further studies of morphological shifts of small vertebrates in fragmented landscapes and the processes that drive such shifts are required to improve our understanding of subtle effects of habitat fragmentation that in the long-run may lead to different levels of species sensitivity to extinction.

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References

Altwegg R, Reyer HU (2003) Patterns of natural selection on size at metamorphosis in water frogs. Evolution 57: 872–882. doi: 10.1111/j.0014-3820.2003.tb00298.x

Ball SL, Baker RL (1996) Predator-induced life history changes: Antipredator behaviour costs or facultative life history shifts? Ecology 77: 1116–1124. doi: 10.2307/1564987

Beachy CK (1995) Effects of larval growth history on metamorphosis in a stream-dwelling salamander (*Desmognathus ochrophaeus*). Journal of Herpetology 29: 375–382. doi: 10.2307/1564987

Becker CG, Fonseca CR, Haddad CFB, Batista RF, Prado PI (2007) Habitat split and the global decline of amphibians. Science 318: 1775–1777. doi: 10.1126/science.1149374

Bell KE, Donnelly ME (2006) Influence of forest fragmentation on community structure of frogs and lizards in Northeastern Costa Rica. Conservation Biology 20: 1750–1760. doi: 10.1111/j.1523-1739.2006.00522.x

Berven KA, Gill DE (1983) Interpreting geographic-variation in life-history traits. American Zoologist 23: 85–97. doi: 10.1093/icb/23.1.85

Buckley CR, Michael SF, Irschick DJ (2005) Early hatching decreases jumping performance in a direct-developing frog, *Eleutherodactylus coqui*. Functional Ecology 19: 67–72. doi: 10.1111/j.0269-8463.2005.00931.x

Delgado-Acevedo J, Restrepo C (2008) The contribution of habitat loss to changes in body size, allometry, and bilateral asymmetry in two *Eleutherodactylus* frogs from Puerto Rico. Conservation Biology 22: 773–782. doi: 10.1111/j.1523-1739.2008.00930.x

Didham RK, Hammond PM, Lawton JH, Eggleton P, Stork NE (1998) Beetle species responses to tropical forest fragmentation. Ecological Monographs 68: 295–323. doi: 10.1890/0012-9615(1998)068[0295:BSRTTF]2.0.CO;2

Dixo M (2005) Diversidade de sapos e lagartos de serrapilheira numa paisagem fragmentada do Planalto Atlântico de São Paulo. PhD Thesis. University of São Paulo.

Dixo M, Metzger JP, Morgante JS, Zamudio KR (2009) Habitat fragmentation reduces genetic diversity and connectivity among toad populations in the Brazilian Atlantic Coastal Forest. Biological Conservation 142: 1560–1569. doi: 10.1016/j.biocon.2008.11.016

Du WG (2006) Phenotypic plasticity in reproductive traits induced by food availability in a lacertid lizard, *Takydromus septentrionalis*. Oikos 112: 363–369. doi: 10.1111/j.0030-1299.2006.13552.x

Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews 81: 117–142. doi: 10.1017/S1464793105006949

Funk WC, Mills LS (2003) Potential causes of population declines in forest fragments in an Amazonian frog. Biological Conservation 111: 205–214. doi: 10.1016/S0006-3207(02)00274-4

Goater CP, Semlitsch RD, Bernasconi MV (1993) Effects of body size and parasite infection on the locomotory performance of juvenile toads, *Bufo bufo*. Oikos 66: 129–136. doi: 10.2307/3545205

Haddad CFB, Prado CPA (2005) Reproductive modes in frogs and their unexpected diversity in the Atlantic Forest of Brazil. Bioscience 55: 207–217. doi: 10.1641/0006-3568(2005)055[0207:RMIFAT]2.0.CO;2

Haddad CFB, Toledo LF, Prado CPA (2008) Anfíbios da Mata Atlântica – Atlantic Forest amphibians. Editora Neotropica, São Paulo, 1–245.

Helle S, Huhta E, Surosa P, Hakkarainen H (2011) Fluctuating asymmetry as a biomarker of habitat fragmentation in an area sensitive passerine, the Eurasian treecreeper (*Certhia familiaris*). Ecological Indicators 11: 861–867. doi: 10.1016/j.ecolind.2010.11.004

Henle K, Davies KF, Kleyer M, Margules C, Settele J (2004) Predictors of species sensitivity to fragmentation. Biodiversity and Conservation 13: 207–251. doi: 10.1023/B:BIOC.0000004319.91643.9e

Heyer WR, Rand AS, da Cruz CAG, Peixoto OL, Nelson CE (1990) Frogs of Boracéia. Arquivos de Zoologia 31: 231–410.

Izecksohn E, de Carvalho-e-Silva SP (2001) Anfíbios do Município do Rio de Janeiro. Editora UFRJ, Rio de Janeiro, 1–148.

Jakob EM, Marshall SD, Uetz GW (1996) Estimating fitness: A comparison of body condition indices. Oikos 77: 61–67. doi: 10.2307/3545585

Janin A, Léna J-P, Jolly P (2011) Beyond occurrence: Body condition and stress hormone as integrative indicators of habitat availability and fragmentation in the common toad. Biological Conservation 144: 1008–1016. doi: 10.1016/j.biocon.2010.12.009

Jessop TS, Madsen T, Sumner J, Rudiharto H, Phillips JA, Ciofi C (2006) Maximum body size among insular Komodo dragon populations covaries with large prey density. Oikos 112: 422–429. doi: 10.1111/j.0030-1299.2006.14371.x

Kaplan RH (1992) Greater maternal investment can decrease offspring survival in the frog *Bombina orientalis*. Ecology 73: 280–288. doi: 10.2307/1938739

Kramer G (1951) Body proportions of mainland and island lizards. Evolution 5: 193–206. doi: 10.2307/2405459

Kwet A, Di-Bernardo M (1999) Anfíbios - Amphibien - Amphibians. EDIPUCRS, Universität Tübingen, Porto Alegre, Tübingen, 1–107.

Laugen AT, Laurila A, Merila J (2002) Maternal and genetic contributions to geographical variation in *Rana temporaria* larval life-history traits. Biological Journal of the Linnean Society 76: 61–70. doi: 10.1111/j.1095-8312.2002.tb01714.x

Laurance WF, Camargo JLC, Luizão RCC, Laurance SG, Pimm SL, Bruna EM, Stouffer PC, Williamson GB, Benítez-Malvido J, Vasconcelos HL, Van Houtan KS, Zartman CE, Boyle SA, Didham RK, Andrade A, Lovejoy TE (2011) The fate of Amazonian forest fragments: A 32-year investigation. Biological Conservation 144: 56–67. doi: 10.1016/j.biocon.2010.09.021

Laurila A, Pakkasmaa S, Crochet PA (2002) Predator-induced plasticity in early life history and morphology in two anuran amphibians. Oecologia 132: 524–530. doi: 10.1007/s00442-002-0984-7

Leary RF, Allendorf FW (1989) Fluctuating asymmetry as an indicator of stress: Implications for conservation biology. Trends in Ecology and Evolution 4(7): 214–217. doi: 10.1016/0169-5347(89)90077-3

Lomolino MV, Perault DR (2007) Body size variation of mammals in a fragmented, temperate rainforest. Conservation Biology 21: 1059–1069. doi: 10.1111/j.1523-1739.2007.00727.x

Losos JB (2009) Lizards in an evolutionary tree: Ecology and adaptive radiation of anoles. University of California Press, Berkeley, 1–528.

Lowe WH, Likens GE, Cosentino BJ (2006) Self-organisation in streams: the relationship between movement behaviour and body condition in a headwater salamander. Freshwater Biology 51: 2052–2062. doi: 10.1111/j.1365-2427.2006.01635.x

Margules CR (1996) Experimental fragmentation. In: Settele J, Margules CR, Poschlod P, Henle K (Eds) Species survival in fragmented landscapes. Kluwer Academic Publishers, Dordrecht, 128–137. doi: 10.1007/978-94-009-0343-2_14

Metzger JP, Alves LF, Goulart W, Godoy Teixeira AM de, Simões SJC, Catharino ELM (2006) An important biological area, but still poorly known: the Morro Grande Forest Reserve. Biota Neotropica 6(2): http://www.biotaneotropica.org.br/v6n2/en/abstract?-article+bn00206022006

Neckel-Oliveira S, Gascon C (2006) Abundance, body size and movement patterns of a tropical treefrog in continuous and fragmented forests in the Brazilian Amazon. Biological Conservation 128: 308–315. doi: 10.1016/j.biocon.2005.09.037

Oliveira AT, Fontes MAL (2000) Patterns of floristic differentiation among Atlantic forests in Southeastern Brazil and the influence of climate. Biotropica 32: 793–810. doi: 10.1111/j.1744-7429.2000.tb00619.x

Pakkasmaa S, Merila J, O'Hara RB (2003) Genetic and maternal effect influences on viability of common frog tadpoles under different environmental conditions. Heredity 91: 117–124. doi: 10.1038/sj.hdy.6800289

Palkovacs EP (2003) Explaining adaptive shifts in body size on islands: A life history approach. Oikos 103: 37–44. doi: 10.1034/j.1600-0706.2003.12502.x

Peig J, Green AJ (2009) New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118: 1883–1891. doi: 10.1111/j.1600-0706.2009.17643.x

Peig J, Green AJ (2010) The paradigm of body condition: A critical reappraisal of current methods based on mass and length. Functional Ecology 24(6): 1323–1332. doi: 10.1111/j.1365-2435.2010.01751.x

Pimm SL, Raven P (2000) Biodiversity - Extinction by numbers. Nature 403: 843–845. doi: 10.1038/35002708

Püttker T, Meyer-Lucht Y, Sommer S (2008) Effects of fragmentation on parasite burden (nematodes) of generalist and specialist small mammal species in secondary forest fragments of the coastal Atlantic Forest, Brazil. Ecological Research 23: 207–215. doi: 10.1007/s11284-007-0366-z

Pyastolova OA, Vershinin VL (1999) Some cytological features of *Rana arvalis* Nilss. frogs on the territory of the Eastern Ural radioactive trace. Russian Journal of Ecology 30: 30–35.

Räsänen K, Laurila A, Merilä J (2005) Maternal investment in egg size: Environment- and population-specific effects on offspring performance. Oecologia 142: 546–553. doi: 10.1007/s00442-004-1762-5

Reading CJ (2007) Linking global warming to amphibian declines through its effects on female body condition and survivorship. Oecologia 151: 125–131. doi: 10.1007/s00442-006-0558-1

Roff DA (1992) The evolution of life histories theory and analysis. Chapman and Hall, London, 1–548.

Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NLR, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. Science 287: 1770–1774. doi: 10.1126/science.287.5459.1770

Sarre S, Wiegand K, Henle K (1996) The conservation biology of a specialist and a generalist gecko in the fragmented landscape of the western Australian wheatbelt. In: Settele J, Margules CR, Poschlod P, Henle K (Eds) Species survival in fragmented landscapes. Kluwer Academic Publishers, Dordrecht, 39–51. doi: 10.1007/978-94-009-0343-2_5

Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: A review. Conservation Biology 5: 18–32. doi: 10.1111/j.1523-1739.1991.tb00384.x

Scheele BC, Boyd CE, Fischer J, Fletcher AW, Hanspach J, Hartel T (2014) Identifying core habitat before it's too late: the case of *Bombina variegata*, an internationally endangered amphibian. Biodiversity and Conservation 23: 775–780. doi: 10.1007/s10531-014-0624-7

Schulte-Hostedde AI, Zinner B, Millar JS, Hickling GJ (2005) Restitution of mass-size residuals: validating body condition indices. Ecology 86: 155–163. doi: 10.1890/04-0232

Semlitsch RD, Scott DE, Pechmann JHK (1988) Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. Ecology 69: 184–192. doi: 10.2307/1943173

Smith DC (1987) Adult recruitment in chorus frogs: Effects of size and date at metamorphosis. Ecology 68: 344–350. doi: 10.2307/1939265

Smith TB, Wayne RK, Girman DJ, Bruford MW (1997) A role for ecotones in generating rainforest biodiversity. Science 276: 1855–1857. doi: 10.1126/science.276.5320.1855

Ståhlberg F, Olsson M, Uller T (2001) Population divergence of developmental thermal optima in Swedish common frogs, *Rana temporaria*. Journal of Evolutionary Biology 14: 755–762. doi: 10.1046/j.1420-9101.2001.00333.x

Stearns SC (1976) Life history tactics: A review of the ideas. Quarterly Review of Biology 51: 3–47. doi: 10.1086/409052

Sumner J, Moritz C, Shine R (1999) Shrinking forest shrinks skink: morphological change in response to rainforest fragmentation in the prickly forest skink (*Gnypetoscincus queenslandiae*). Biological Conservation 91: 159–167. doi: 10.1016/S0006-3207(99)00089-0

Thomas CD, Hill JK, Lewis OT (1998) Evolutionary consequences of habitat fragmentation in a localized butterfly. Journal of Animal Ecology 67: 485–497. doi: 10.1046/j.1365-2656.1998.00213.x

Tocher MD, Gascon C, Zimmerman BL (1997) Fragmentation effects on a Central Amazonian frog community: A ten year study. In: Laurance WF, Bierregaard RO (Eds) Tropical forest remnants: Ecology, management, and conservation of fragmented communities. The University of Chicago Press, Chicago, 124–137.

Toft AT (1985) Resource partitioning in amphibians and reptiles. Copeia 1985(1): 1–21. doi: 10.2307/1444785

Tucker DB, McBrayer LD, Harrison JS (2014) Population structure of Florida scrub lizards (*Sceloporus woodi*) in an anthropogenically fragmented forest. Herpetologica 70(3): 266–278. doi: 10.1655/HERPETOLOGICA-D-13-00041

Wade MJ (2004) Selection in metapopulations: The coevolution of phenotype and context. In: Hanski I, Gaggiotti OE (Eds) Ecology, genetics, and evolution of metapopulations. Elsevier Academic Press, Amsterdam, 259–274. doi: 10.1016/B978-012323448-3/50013-1

Wells KD (2007) The Ecology and Behavior of Amphibians. University of Chicago Press, Chicago. doi: 10.7208/chicago/9780226893334.001.0001

Wiegand K, Sarre S, Henle K, Stephan T, Wissel C, Brandl R (2001) Demographic stochasticity does not predict persistence of gecko populations. Ecological Applications 11: 1738–1749. doi: 10.1890/1051-0761(2001)011[1738:DSDNPP]2.0.CO;2

Wu Z, Li Y, Murray BR (2006) Insular shifts in body size of rice frogs in the Zhoushan archipelago, China. Journal of Animal Ecology 75: 1071–1080. doi: 10.1111/j.1365-2656.2006.01126.x